

4. Soil Biodiversity

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There is considerable uncertainty as to the effect of global change on soil biodiversity. This is primarily due to a tremendous lack of knowledge of soil organisms. The sheer abundance of species in the soil (millions·m⁻²), our naïvete of soil biodiversity at the species or molecular level for groups such as bacteria, fungi, and microinvertebrates, the complexity of relationships of soil biodiversity to vegetation type and ecosystem functioning, and the limited studies on the effect of long-term elevated atmospheric CO₂ and soil warming on soil species diversity contribute to our uncertainty of the impact of global change drivers on soil biodiversity. Nevertheless, there is sufficient evidence to indicate that the composition and abundance of many groups of soil biota are affected, at local and regional scales, by changes in vegetation, soil physical and chemical habitat, climate, and invasive species (Bongers 1990; Ruess 1995). These changes in soil biota are important because they are linked to critical ecosystem processes that sustain life. Soil degradation has accelerated globally as human populations have expanded, threatening the stability of Earth's ecosystems. Determining how soil species diversity will change under global change drivers will help scientists, policy makers, and managers devise and implement strategies to preserve and maintain our terrestrial ecosystems for the long term.

We developed global scenarios of soil biodiversity change and the possible effects on ecosystem functioning for the year 2050 by using the current knowledge on, (1) the wealth of soil biodiversity and its functions in ecosystems (Table 4.1, 4.2), (2) the factors that determine soil biodiversity (Fig. 4.1),

Table 4.1. Major phyla found in soils, in order of increasing body width; their functions in ecosystems, number of species described to date in soil habitats and estimated total number of species that exist in all habitats (terrestrial and aquatic). Species in litter and decaying wood are included in estimates of soil-dwelling species

Body width	Taxonomic group	Function in ecosystem	Described soil species	Reference for described species	Estimated number of species in all habitats	Reference for estimated number of species
1–2 µm	Bacteria	decay; trace gas producers & consumers; N fixers; pathogens; biocontrol	13,000	(Torsvik et al. 1994) (Akimov and Hattori 1996)	1,000,000	(Hammond et al. 1995)
3–100 µm	Fungi	decay; pathogens; plant symbionts; biocontrol	18,000–35,000	(Brussaard et al. 1997)	1,500,000	(Hammond et al. 1995)
15–100 µm	Protozoa	regulate bacterial growth; increase N availability; predators	1,500	(Brussaard et al. 1997)	200,000	(Hammond et al. 1995)
5–120 µm	Nematoda (roundworms)	increase N availability; feed on bacteria, fungi, soil algae, small fauna, plant & animal parasites, & pathogens enhance microbe growth; disperse microbes	5,000	(Brussaard et al. 1997)	400,000–10,000,000	(Hammond et al. 1995)
80 µm–2 mm	Acari (mites)	feed on bacteria, fungi plants, small fauna; parasites; enhance microbe growth; disperse microbes	20,000–30,000	(Brussaard et al. 1997)	900,000	(www1)
150 µm–2 mm	Collembola (springtails)	fungivores; predators; detritivores; feed on algae	6,500	(Brussaard et al. 1997)	24,000	(www2)
300 µm–1 mm	Diplura	fungivores; predators; detritivores	660, 800 ^a	(www3; www4)	1,600	(www3)

500 µm–4 mm	Symphyla	detritivores; plant-feeders	160 ^b	(Scheller 1982)	No estimate	(Behan-Pelletier pers. comm.)
	Enchytraeidae (pot worms)	detritivores; bioturbators; enhance microbial growth; disperse microbes	600	(Brussaard et al. 1997)	1,200	
500 µm–4 mm	Isopoda (termites)	bioturbators; aid soil structure; soil and wood feeders; enhance microbial growth; mounds are habitat for biota	1,600	(Bignell pers. comm.; Bignell and Eggleton 1998)	3,000	(Bignell pers. comm.; Bignell and Eggleton 1998)
	Formicoidea (ants)	bioturbators; enhance microbial growth; hill are habitat for biota; aid soil structure	8,800	(Brussaard et al. 1997)	15,000	(Brown 1982)
2–20 mm	Isopoda (sowbugs, pillbugs)	bioturbators; predators; detritivores; herbivores; microbivores	5,000	(www5)	No estimate	
1–50 mm	Chilopoda (centipedes)	predators; mix soil & litter	2,500 ^c	(Hoffman 1982)	No estimate	
1–50 mm	Diplopoda (millipedes)	detritivores; calcium cycling; mix soil & litter	10,000 ^d	(Hoffman 1990)	60,000	(Hoffman 1990)
	Oligochaete (earthworms)	consume, mix soil & litter; reconstitute litter aid soil structure	3,600	(Brussaard et al. 1997)	No estimate	
	Diptera larvae (flies, blackflies)	plant & animal parasites; predators; decay dung	60,000 ^e	(McAlpine 1990)	240,000	(www6)

^a The majority of Dipluran species are in soil (Maddison 1997). Thus, the number of described soil-dwelling Diptera species described was assumed to be equal to the total number described.

^b Symphyla live in soil and litter (Scheller 1982); thus, the number of described soil-dwelling species was assumed to be equal to the total number described.

^c Chilopoda live in soil, leaf litter, rotting woods and caves (Maddison 1997); thus, the number of described soil and litter dwelling species was assumed to equal the total number of described species.

^d Diplopoda are characteristic of the upper soil and litter horizons (Hoffman 1990); thus, the number of described soil and litter-dwelling species was assumed to be equal to the total number described.

^e We calculated the number of described species in soils based on McAlpine's estimate (McAlpine 1990) for the United States that 50% of Diptera species are in soils.

Table 4.2. Ecosystem services provided by soil biota^a

Regulation of major biogeochemical cycles
Retention and delivery of nutrients to plants
Generation and renewal of soil structure and soil fertility
Bioremediation of wastes and pollutants
Provision of drinking water
Modification of the hydrological cycle
Mitigation of floods & droughts
Erosion control
Translocation of nutrients, particles and gases
Regulation of atmospheric trace gases (e.g., CO ₂ , NO _x) (production and consumption)
Modification of anthropogenically driven global change (e.g., carbon sequestration modifiers of plant responses)
Regulation of animal and plant populations
Control of potential agricultural pests
Contribution to all plant production for food, fuel and fiber

Determinants of landscape heterogeneity
Vital component of habitats important for recreation and natural history

^a Modified from Bengtsson et al. 1997; Daily 1997; Wall and Virginia 1999.

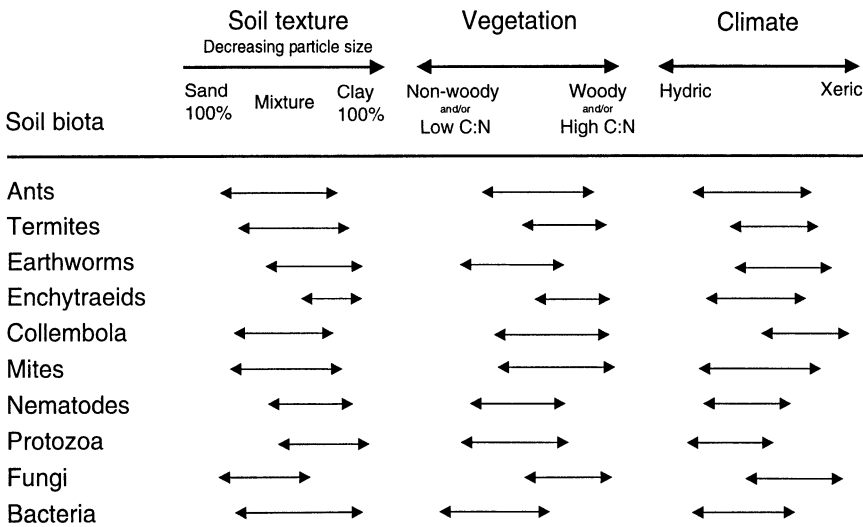


Figure 4.1. Species diversity for most groups of soil biota is strongly affected by global change drivers altering the three determinants of soil biodiversity, soil texture, vegetation, and climate. For each group arrows represent the range where highest biodiversity occurs at a global scale under soil texture [pure sand-100%; a mixture of particle sizes (e.g., sand, silt, and clay), and almost 100% pure clay], vegetation (low to high C:N and nonwoody-to-woody) and climate (hydric to xeric).

(3) the range of conditions over which the highest biodiversity occurs for selected soil groups (Fig. 4.1), and (4) the effects of five drivers of global change—changes in land use, climate, atmospheric CO₂ concentration, nitrogen deposition and acid rain, and introduced species—on soil biodiversity or the factors that determine it. We then ranked the drivers by the impact they would have on the highest biodiversity. This provides the global change scenarios most likely to affect soil biodiversity at the species level (Fig. 4.2) that would have an impact on ecosystem processes.

Soil Biodiversity

Representatives of all above-ground phyla, from chordates [e.g., gophers, prairie dogs (Andersen 1987; Holland and Detling 1990) and caecilians

Soil biota	Δ Land use	Elevated CO ₂ Δ Climate (Vegetation change)	Biotic introductions
Ants	****	***	****
Termites	*****	*****	****
Earthworms	*****	***	*****
Enchytraeids	*****	*****	*****
Collembola	***	****	***
Mites	****	****	***
Nematodes	****	****	****
Protozoa	**	***	****
Fungi	***	****	****
Bacteria	**	***	***

Figure 4.2. Land use change, elevated CO₂, and biotic exchange will have the most profound impacts on soil biodiversity, but the impacts will differ with the group of organisms shown. Land use change has a radical impact on soil biodiversity because it affects the three determinants of soil biodiversity shown in Figure 4.1. Land use change will have the most visible impact on the entire soil biota. The greatest effect will be seen more quickly on the macrofaunal groups (e.g., termites, earthworms, enchytraeids) because of their effects on ecosystem function (e.g., change in soil structure, increased erosion, change in rate of wood decomposition, changes in hydrology, changes in carbon, and nitrogen fluxes). The effects of elevated CO₂ will be mediated indirectly through changes in one determinant of soil biodiversity, vegetation (Fig. 4.1). Organisms restricted by climate and vegetation will be most affected and include termites, and enchytraeids, with lesser effects on soil mesofauna and fungi. Biotic introductions of plants and other soil organisms will have critical effects on two determinants of soil biodiversity (i.e., soil texture and vegetation) and will cause the greatest changes in the diversity of earthworms and enchytraeids.

(Wake 1993)], to molluscs, arthropods, nematodes, mites and microbes, and from vascular plant roots to algae, are found in subsurface habitats. Some of these groups are listed in Table 4.1. The number of described species in soil represents a small fraction of the estimated total number of discovered soil species. Many scientists predict that there are a greater number of species in soil than above ground (Anderson 1995; Hammond et al. 1995). The high number of species, the complexity of their interactions below ground, and linkages to above ground (Bardgett et al. 1988; Hooper et al. in press), and the difficulty in determining species' contributions to ecosystem processes, has made predictions of their response to environmental change at local and regional scales a tremendous challenge for soil ecologists.

Stotzky and Bollag (1992) noted, "Soil is the most complex of microbial habitats." There is, as yet, no location with a complete species list of all soil organisms, or even a location with a species list of all soil invertebrates. Identifying the total number of species within a given soil for any ecosystem has been hampered by many of the same problems found in assessing biodiversity for above-ground systems (Blair et al. 1996; Wall and Virginia 1999). For example, many identification keys are based exclusively on the adult morphological and biological (life cycle) characteristics; thus, juveniles may be misidentified as a "new" species. As with above ground, many species within a taxonomic group are rare (Bills and Polishook 1994; Price and Siddiqi 1994), the species associations with habitat and other organisms are poorly known, making "hunting" for a species difficult, and migratory and dispersal mechanisms vary with species and taxonomic group.

Determining the influence of global change drivers on soils and soil biodiversity must include consideration of the spatial and temporal scales the organisms use. The spatial habitat varies with the organism's biology and size. Local scales defined for smaller species and the molecular level (e.g., bacteria, fungi, protozoa, nematodes) as a gram of soil may be, for larger species (e.g., gophers, molluscs, ants, millipedes, ectomycorrhizae), meters of soil. The scientist's choice of sampling and extraction methods can affect the biodiversity of the animals retrieved from soil; therefore, methods should be considered when comparing biodiversity across larger scales. Temporal scale considerations (Moore and de Ruiter 1991), such as whether the species migrates centimeters to meters vertically within the soil profile on a diurnal or seasonal basis, or whether it is a transient soil resident (e.g., an invertebrate with part of its life cycle in soil), can influence species diversity estimates. Changes in season, climate, plant species composition, and phenology of plants similarly contribute to changes in the temporal patterns of soil biodiversity.

Major limitations to determining species diversity in soils have been the minimal, and still declining, taxonomic expertise as well as the amount of labor involved in sampling, extraction, and identification of the soil biota. In a Cameroon soil study (Lawton et al. 1998) more than 90% of the nematodes were unidentified because of the labor, time, and cost constraints. Despite these difficulties, melding of technology (e.g., GIS maps of soil types, soil

carbon, moisture and vegetation, stable isotope techniques, molecular biology, and microscopic video images for www display) along with interdisciplinary advances are accelerating our understanding of soil biodiversity across temporal and spatial scales (Behan-Pelletier and Newton 1999). Molecular techniques, often combined with morphological techniques, expand our ability to identify species and molecular types for microbial, fungal, and invertebrate groups, and to determine their distribution across geographic scales. These tools also result in discoveries of new key groups of microorganisms (Dedysh et al. 1998) and relationships among invertebrates (Blaxter 1998; Blaxter et al. 1998). Direct field measurements relating ecosystem processes to soil species diversity [e.g., use of stable isotopes to measure carbon and nitrogen fluxes in individual soil invertebrates (Hobbie et al. 1998), electron probe microanalysis, and laser microprobe microanalysis] are emerging as necessary tools for soil ecology. These and other approaches, combined with global change models (Smith et al. 1998), increase our ability to predict the response of soil biodiversity and ecosystem processes to global change drivers.

Soil Species and Ecosystem Processes

Ecosystem services provided by soil organisms are numerous and critical to human existence (Table 4.2). Information on the role of soil species in global ecosystem processes derives from two disciplines: ecosystem science, where research focuses on the functional or trophic group level, and agricultural sciences, where research focuses at the species level. The synthesis of the two approaches is generating a greater understanding of the potential responses of soil species to global change. The services attributable to soil biota (Table 4.2) include: maintenance of soil fertility, decomposition of organic matter, cycling of nitrogen and carbon, influencing plant fitness through symbiotic, mutualistic, and parasitic associations (Freckman and Caswell 1985; Schimel and Gullledge 1998; Wall and Moore 1999), channeling and moving soil organic matter and other biota horizontally and vertically in the soil, thus affecting hydrology, aggregation of soil particles and soil stability (Lynch and Bragg 1985; Hendrix et al. 1990; Gupta 1994; Lavelle et al. 1994b; Linden et al. 1994; Lavelle et al. 1997), and contributing to clean air and water by degrading pollutants (Coleman and Crossley 1996; Daily et al. 1997; Freckman et al. 1997; Hooper and Vitousek 1998). There has been increasing interest in how soil species diversity structures above-ground plant communities (van der Heijden et al. 1998). In addition, the soil biota serve as food sources, predators, parasites, and biological control agents for plants and animals above and below ground (Gaugler and Campbell 1991; Beckage 1998; Strong 1998). In performing these functions, soil biota are an integral link to other organisms, vertically to above-ground systems, and horizontally to sediments of freshwater and marine ecosystems (Groffman and Bohlen 1988; Freckman et al. 1997; Wall Freckman et al. 1997; Wagener et al. 1998).

Ecosystem research has simplified the vast diversity of the soil biota in order to clarify their role in ecosystems by categorizing them into functional groups, each containing many species of similar morphologies, physiologies, and food sources. Functional groups in soil foodwebs can include primary producers, plant parasites and pathogens, fungal and bacterial decomposers, fungal symbionts, methanogens, nitrogen-fixing bacteria, fungal and bacterial feeders, predators, and omnivores. A consequence of this simplification is that all species of a functional group (e.g., fungal-feeding mites) are considered as processing their food base (carbon, nitrogen) at the same rate, excreting at the same rate, and metabolizing at the same rate.

The functional group approach has permitted exploration of the overall role of soil organisms in ecosystem processes (e.g., decomposition and nutrient flux). Although it ignores species differences, it has yielded valuable findings. Results of the International Biological Program (IBP) showed soil fauna were minor players in the energetics of global terrestrial ecosystems, contributing less than 5% to total soil respiration (Petersen and Luxton 1982). Since then, numerous experimental studies combined with below-ground foodweb models (Hunt et al. 1987; Paustian and Schnurer 1987b; de Ruiter et al. 1993; Smith et al. 1998) involving earthworms and other soil fauna, altogether have shown important effects on other ecosystem processes such as nutrient cycling, herbivory, and trace gas fluxes (Brussaard et al. 1997). Hunt et al. (1987) showed in the shortgrass steppe that bacterial feeding nematodes and amoebae, previously thought to be less significant than other biota in assessments of energetics of the soil community, contributed 83% of the total N mineralization attributed to soil invertebrates. Lauenroth and Milchunas (1991) estimated that one third of the herbivory in the same ecosystem was due to plant parasitic nematodes.

Thus, ecosystem science has provided a backbone for clarifying the role of soil functional groups in ecosystem processes and shown the pivotal linkages among functional groups within the soil foodweb to above-ground systems (Freckman et al. 1997). As with above-ground biota, disturbance of one species may have an indirect or “domino” effect on other soil species within the same, or across different, functional groups. This confounds our ability to predict the effect of global change drivers on soil biodiversity, and, subsequently, changes in ecosystem processes (Coleman et al. 1992; Anderson 1995; Ettema 1997; Giller et al. 1997; Lavelle et al. 1997; Swift 1997; Ettema 1998; Ingram and Wall-Freckman 1998; Swift et al. 1998; Wardle et al. 1998).

Just as the use of functional groups was an important step for evaluating the functions of groups of species in ecosystems, agricultural science also made significant contributions to ecosystem research. This has revealed that species within the same functional group and even within the same genus have varying morphologies, life strategies, and, consequently, varying responses to microhabitat changes. These studies disclose the extent of differences in species’ responses within a functional group and the direct (Table 4.3) and feedback effects they have on plant communities. For example, trophically

Table 4.3. Direct effects of some soil organisms on plants

Root Organism	Effect on Plant
Bacterial symbionts (<i>Rhizobia</i> , actinorhizas)	Symbiotic nitrogen fixation; sink for photosynthate
Bacterial pathogens <i>Pseudomonas solanacearum</i>	Causes bacteria wilt of solanaceous crops (Walker 1969)
<i>Agrobacterium tumefaciens</i>	Causes crown gall of apple, peach, apricot, grape, etc. (Walker 1969)
<i>Streptomyces scabies</i>	Causes common scab of potato (Walker 1969)
Fungal symbionts (ecto- and endomycorrhizae)	Symbiotic resource capture—increases plant tolerance to water and osmotic stress; increased P uptake; sink for photosynthate: (Bowen 1978; Allen 1991) may protect from pathogenic fungi (Newsham et al. 1995)
Fungal pathogens (e.g., <i>Rhizoctonia</i> and <i>Phytophthora</i>)	Kill root seedlings, infect vascular system, decrease plant growth, cause root rot, increase exudation (Walker 1969; Van Gundy et al. 1977)
Fungal endophytes	Causes enhanced tillering and root growth grasses, increases drought tolerance, protect against pathogens and herbivory, (beneficial to plants) (Schardl and Phillips 1997).
Nematode pathogens <i>Pratylenchus penetrans</i> on alfalfa	Changes root architecture, plant nutrient and water uptake and translocation, decreases root biomass. Plants may exhibit no apparent damage, or crop loss.
<i>Bursaphelenchus xylophilus</i> on pine trees	Increases proliferation of lateral roots, decreases tree growth, causes pine wilt, and kills trees.
<i>Aphelenchoides fragariae</i>	Foliar parasite, discolors leaves, kills cells.
Arthropods	
Beetles (Scarabaeidae, Elateridae) <i>Diabrotica</i> spp.	Feeds on roots (corn rootworm) (Gerson 1996)
Scale insects <i>Daktulosphaira vitifoliae</i>	Grape phylloxera, root sucking insect, feeds on vine roots, can cause galls (Bournier 1977)

similar nematode species respond differently to soil disturbance because of variable ingestion and metabolic rates (minutes to hours) (Schiemer 1983; Ferris et al. 1995; Ferris et al. 1996; Ferris et al. 1997), and generation times (weeks to months) (Ettema and Bongers 1993; Venette and Ferris 1997; Ettema 1998). Soil species within the same genus have differing effects on plants (Table 4.3), and thus different effects on crop production and economics. The response of a plant species to soil pathogens, even within the same genus, can be very specific and is used as a tool for diagnosing plant pathogens and symbionts and determining management alternatives (Cook and Baker 1983; Yeates 1999). Root architecture of the same plant species will change depending on the species of nematode parasitizing the root. The plant response to a root pathogen may also be noted above ground with changes in plant morphology (e.g., size of fruit, plant growth), plant metabolism (e.g., leaf respiration, nutrient status), and plant death.

Agricultural science has provided evidence that: (1) soil species within the same trophic group respond differently to changes in the above- or below-ground environment, (2) trophically similar species can induce different responses in plants, and (3) changing plant species (e.g., in crop rotation) and plant litter inputs (e.g., in no-tillage systems) can affect both individual plant root pathogens, or biocontrol organisms, and the structure of the entire soil community. Thus, we suggest that for global change scenarios predicting changes in vegetation (e.g., species composition) metabolism (NPP, carbon allocation), litter quality, quantity, and morphology (root architecture), soil biodiversity will be affected at the species and molecular level. Further, because of the differential effects at the soil species and DNA level, scenarios of global change influencing climate, plants and the soil physicochemical environment cannot be accurately predicted by examining soil biodiversity only at the functional or trophic group level. Moreover, the magnitude of these global change effects on soil species diversity will be interlocked with the time scale (e.g., the abruptness of the vegetation change), which adds to the difficulty in predicting the response of soil biodiversity to global change drivers. Studies determining the effect of future scenarios of soil biodiversity under global change will need to incorporate knowledge of species and their contribution to ecosystem processes, across temporal and spatial scales.

Geographical Patterns

Geographical patterns of soil biodiversity are poorly known (Brussaard et al. 1997). The International Biological Program (Petersen and Luxton 1982) was perhaps the closest to a global soil biodiversity synthesis (i.e., an estimate of how many and which taxonomic and functional groups exist in biomes across the globe). The objective of the IBP, however, was to obtain results on the contribution of soil fauna functional groups to ecosystem energetics rather

than a taxonomic species diversity comparison across biomes. Syntheses of species biogeography have been developed for several years for some above-ground taxa (e.g., for flowering plants, see Williams 1964, Ricklefs et al. 1995), but they are generally lacking for soil biota. Assessments of soil biodiversity exist for some countries (Szegi 1984; Dighton and Jones 1994), but the few global assessments of soil biodiversity are mostly for only a few components of the vast diversity in soils, generally the larger soil organisms (e.g., ants, termites, earthworms) (Pearce and Waite 1994; Blair et al. 1995; Brussaard et al. 1997; Folgarait 1998).

Assumptions that species richness declines at the poles ignores below-ground complexity (Mooney et al. 1995; Ricklefs et al. 1995; Brussaard et al. 1997; Boag and Yeates 1998). Global biogeographic patterns based on limited data must be evaluated carefully for each group of soil biota. Termite and ant diversity declines with distance from the equator, but this pattern is not assured for earthworms, enchytraeids, mites, and nematodes (Lavelle 1993; Lavelle et al. 1994b; Brussaard et al. 1997; Folgarait 1998). Earthworms vary along a thermolatitudinal gradient, and are absent from dry ecosystems (Lavelle et al. 1997). The number of mite species was similar in tropical South American and temperate North American sites (Stanton 1979; Heneghan et al. 1998). For nematodes, where there often are more than 100 rare species in a soil sample, Procter (1984, 1990) and Boag and Yeates (1998) suggested a greater diversity in temperate than tropical latitudes; however, other data show greater species richness in a Cameroon site (Lawton et al. 1996; Bloemers et al. 1997; Lawton et al. 1998). Even ant diversity that follows the latitudinal pattern declines with altitude and aridity (Folgarait 1998).

Establishing biogeographical patterns for soil organisms is difficult. Species overlap between soil samples taken within the same ecosystem can be low, particularly for microscopic organisms (e.g., mites, Collembola, nematodes, tardigrades, protozoa, bacteria, fungi). For example, less than 6% of the total nematode species were common to 50 cores collected within the same ecosystem (Price and Siddiqi 1994). Ettema (1998) notes that because nematode diversity is significantly patchy at the local scale of soil cores, as well as at regional and ecosystem levels, patchiness occurs across all scales (see also Robertson and Freckman 1995). Communication via the internet increases opportunities for syntheses of geographical distribution patterns (e.g., Collembola; <http://www.geocities.com/~fransjanssens/>).

The lack of syntheses on distribution patterns for the entire soil biota (Table 4.1) limits our ability to predict how soil species diversity and soil communities will vary with biome, climate, and vegetation on regional to global scales. Many species are cosmopolitan, and many regions have endemic species (daGama et al. 1997; Wall Freckman and Virginia 1998), but we have been unable to identify traits that allow a species to be either cosmopolitan or endemic. A greater understanding of biogeographic patterns and the mechanisms determining habitat ranges will allow better predictions of species loss, species introductions, the identities of species needed for restora-

tion and maintenance of soils, and the effect of global change on subsurface biota that are involved in transfers of materials between ecosystems. As we currently probe the impact of global change scenarios on species diversity and biome shifts and develop management plans for sustainable soils, we rely on limited knowledge of ca. 5–10% of the soil species (Brussaard et al. 1997; Wall and Virginia 1999).

Determinants of Soil Biodiversity

The abundance and structure of the soil community at the global scale are determined by: (1) vegetation, (2) soil physical and chemical properties, (3) microclimate, and (4) the interactions among soil organisms (Swift et al. 1979; Anderson 1995; Giller et al. 1997). These factors are integrated over geologic time, making it difficult to determine whether a change in one factor will result in a corresponding change in soil biodiversity.

On a global and regional scale, vegetation is the primary determinant of soil biodiversity. Numerous studies have shown decreasing soil organism abundance and diversity away from plants (Ingham et al. 1985; Freckman and Mankau 1986; Yeates 1987; Ingham et al. 1989; Yeates and Orchard 1993; McSorley and Frederick 1996). Plants influence the composition of the soil community through both root and above-ground organic inputs and changes in soil microclimate (e.g., moisture, temperature, oxygen content, etc.). Plant biomass, the quantity and quality of the litter (C, N, lignin) (Fig. 4.1), the plant species community composition, and the functional composition of plants (C_3 , C_4) all contribute to structuring soil communities (Lawton et al. 1998; Hooper et al. 2000). For example, input of organic matter from vegetation with lower C:N ratios and less lignin results in decomposition by a bacterial-based foodweb, whereas a presence of a greater amount of plant structural material (e.g., lignin and cellulose) results in decay by a fungal-based foodweb (Paustian and Schnurer 1987a,b; Christensen 1989). Plant phenology, root architecture, depth of rooting, and plant metabolism, including reallocation of carbon within the plant, add to the multiplicity of factors that affect soil biodiversity. On a global and regional basis, the vegetation shifts predicted by global change models will indirectly impact soil species diversity, and the feedback effects on global ecosystem processes are unknown.

Soil physical and chemical properties provide the habitat for soil organisms and include soil texture (the combination of sand, silt, and clay) (Fig. 4.1), moisture, salinity, pH, organic carbon, and N, P, K. Soil physical structure determines both the space and boundaries for organisms and the habitat temperature and moisture dynamics for the species that coexist in that habitat (Wallace 1963; Sohlenius 1985; Robertson and Freckman 1995). Organic matter, soil chemistry, and legacies of soil changes due to historical land use modify the range of soil textures and thus influence soil biodiversity. On a global scale, for example, mite diversity is generally higher in well-structured

soils with high organic matter, and lower in soils with a sandy texture of limited organic matter (Walter 1999). Based on literature and personal communication with taxonomic experts, we hypothesize that on a global basis, the diversity of invertebrates (e.g., ants, termites, earthworms, and enchytraeids) will be higher in soils that have a greater soil textural diversity as compared with soils of nearly pure sand or pure clay (Fig. 4.1).

Adding to the complexity of factors that influence geographic patterns of soil biodiversity at the regional level is the influence of geologic history on soils. Earthworm distribution in North America has been defined by glaciation, with species moving into areas of the Wisconsinian Glaciation (Gates 1982; James 1990, 1995). Enchytraeids have replaced earthworms in many tundra, boreal forests, and northern parts of temperate zones. Soil biodiversity in the Antarctic Dry Valleys appears to be structured by legacy carbon left from ancient lakes, soil salinity, and soil moisture (Wall Freckman and Virginia 1998; Burkins et al. 2000; Virginia and Wall 1999).

Microscale soil texture characteristics at the patch and microscale can influence trophic dynamics. Robertson and Freckman (1995) used geostatistics to examine the spatial variation of nematode trophic groups across cultivated ecosystems and found that soil texture and pH explained the patchy distribution of all groups except plant parasites at meters to hectare scales. At the microhabitat scale, Elliott et al. (1980) noted little competition between bacterial-feeding protozoa and nematodes for their food source, bacteria, because protozoa access bacteria in soil textures with smaller-sized soil pores than do nematodes. Thus, a mixture of textures would allow for greater diversity of biota.

Physical disturbance to soils decreases soil biodiversity (Paoletti et al. 1992; Freckman and Ettema 1993; Lavelle et al. 1994a). Physical disturbances that change soil structure (e.g., plowing, loss of topsoil through water and wind erosion) have a rippling effect on other factors defining the organism's habitat, such as soil moisture, oxygen availability, and soil chemistry. For example, soil texture compaction differentially affects invertebrates (Whalley et al. 1995) and vertebrates (e.g., caecilians, gophers, prairie dogs) (Andersen 1987; Ducey et al. 1993). The loss of species and resulting impact on ecosystem processes is more obvious for larger invertebrates (e.g., earthworms, termites, and ants), whose diversity is narrowly defined by soil parameters such as texture (Sochtig and Larink 1992) (Fig. 4.1).

Regional climate patterns (e.g., water, temperature, wind) contribute to the distribution patterns of soil organisms (Swift et al. 1979). Enchytraeids and earthworms are absent in dry and desert ecosystems, and in cold, acid water-logged regions of the world (Blair et al. 1995; Lavelle et al. 1997). Climate changes that result in drier surface soils affect the seasonal distribution patterns of enchytraeids in soils, and increase their densities at depth (Springett et al. 1970; Briones et al. 1997). The distribution of some plant parasitic nematode species in the UK can be explained by their relationship to isotherms (Boag et al. 1991) and plant type (e.g., deciduous, coniferous,

grasses) (Boag 1974; Boag and Williams 1976). Young et al. (1998) suggest that freezing–thawing events predicted by global-change models affect soil particle size distribution and thus have an influence on local-scale soil species diversity.

Rainfall patterns could shift soil community composition dramatically on a regional basis, directly or indirectly, through changes in vegetation. Flooding can be essential for the life cycle of many species, even if it occurs rarely. In the playas of the southwestern United States deserts, brine shrimp that inhabit the soil in an egg state for years, suddenly appear active with flooding (Crawford 1981); alternatively, flooding events can create anaerobic soil conditions that affect species composition.

Effects of Global Change Drivers

Although soil biodiversity may be determined by factors other than, or in addition to, the three major factors we have selected (Fig. 4.1), we considered the soil biota holistically and in the context of those factors that determine distribution and diversity. We asked, under what conditions (i.e., soil structure, vegetation, and climate) will there be the greatest phyla and species diversity and which of these groups might be more vulnerable to global change drivers? Representative groups that are known to affect ecosystem processes were used in Figure 4.1. We approached this task cautiously because for many groups, such as nematodes, protozoa, bacteria, and fungi, there are few data on the relationship of diversity to soil texture, vegetation type, or climatic regime.

Those global change drivers that affect the soil physical and chemical properties, vegetation, and climate and shift them between conditions that support high versus low biodiversity over the largest land area (e.g., regional, biome, landscape, and continental) will have the greatest influence on future soil biodiversity. These will probably be land use change, elevated CO₂ and climate change (through vegetation change), and biotic exchange (Fig. 4.2). In comparison, nitrogen deposition and soil warming will affect species-level diversity to a lesser extent. We are aware that interactions among these factors (e.g., among water and vegetation) can be simultaneous and additive, yet subject to a time lag due to migration and dispersal limitations, and the like. This adds to the challenge of predicting the effect of global change drivers on soil biodiversity at large spatial scales.

Effects of global change drivers on soil biodiversity are described in greater detail later, but we expect land use change to have the greatest impact because it radically alters the three most important determinants of diversity (e.g., soil structure, vegetation, and microclimate). Evidence strongly suggests that the species diversity of all soil taxa decreases precipitously with land use change. Land use change is a physical disturbance that results in vegetation change and the disruption of soil habitats, thus changing the organic inputs

to soil and altering the decomposition foodweb. This, in turn, affects plant roots and the herbivorous foodweb. Effects on climate at micro-, local, and regional scales are linked with these changes. We would expect the diversity of termites, earthworms, and enchytraeids to be most affected because their diversity is confined to a small range of soil textures. Bacteria would be the least affected because their diversity, although just beginning to be discovered, appears to occur across a broad spectrum of soil textures, plant communities, and climate.

Elevated CO₂ and climate change will have major effects on soil biodiversity indirectly through vegetation change (e.g., plant metabolism and plant community composition). Based on experiments at the functional group level, we expect that, if below-ground plant resources (no change in plant species) increase, the abundance of bacterial and fungal foodwebs, root pathogen populations, and herbivory will increase. It is unclear if these increased carbon inputs will affect biodiversity; however, root pathogen diversity (e.g., obligate parasites: fungi, bacteria, plant-parasitic nematodes) and symbiont diversity (mycorrhizae, rhizobia), is expected to decline with any sudden change in plant composition that results in nonhost plants. Those organisms (e.g., ants, termites, enchytraeids) whose highest diversity is constrained by climate and/or confined to an extreme of vegetation types (either woody or non woody) (Fig. 4.1) would be expected to have greater changes in diversity, with perhaps a decline in diversity, if vegetation types were switched to the other under elevated CO₂ and climate change (Fig. 4.2).

As a global change driver, biotic introductions of animals, plants, and microbes have had, and will continue to have, a devastating effect on soil biodiversity (Fig. 4.2). Introductions of plant species change the soil habitat, root-symbiotic and pathogenic relationships, hydrology, and organic matter inputs to the soil. For plant introductions, we would predict the greatest changes in diversity for termites, enchytraeids, bacterial and fungal symbionts (e.g., rhizobia, mycorrhizae), and root pathogens (Fig. 4.2). Because of their impacts on soil physical and chemical habitats invasive soil macroinvertebrates (e.g., ants, termites, earthworms) are predicted to have major repercussions on the diversity of soil mesofauna, bacteria, and fungi.

Studies on atmospheric deposition (primarily sulfate and nitrate) showed effects on soil chemistry and diversity (Huhta 1984; Bewley and Parkinson 1986; Persson et al. 1989; Baath et al. 1990; Hyvonen and Persson 1990). We would expect aquatic soil animals confined to nonporous, less drained and more clay soils (earthworms, enchytraeids, nematodes, protozoa), as well as bacteria and fungi, to have decreased biodiversity globally because of changes in water chemistry due to increased atmospheric nitrogen deposition.

Soil warming experiments have shown differential effects on groups of soil taxa at local scales. The mechanisms by which warming effects taxa include direct climatic effects (e.g., increased temperature on soil habitats) and altered wet-drying frequency cycle that affects migration, dispersal and life histories. Because warming can affect both hydric and xeric (Fig. 4.1) habitats, we made

no prediction as to which biotic group will be most affected at larger scales. Polar regions, however, may lose a key group—enchytraeids—with warming, but they may also gain in overall soil biodiversity.

Land Use Change

Accelerating destruction of soils through conversion of land for human use will be the primary driver that impacts soil biodiversity because of its strong effect on soil physical and chemical properties, vegetation, and microclimate (Sochtig and Larink 1992; Murphy et al. 1995; Brussaard et al. 1997; Lavelle et al. 1997). In general, we expect that land conversion to regrowth forests, agriculture and cities will destroy lineages of soil species and the multiplicity of their interactions at the regional scale. The disturbance to soil taxa and soil community structure has been recorded in many ecosystems (Freckman and Ettema 1993; Brussaard et al. 1997; Lavelle et al. 1997; Folgarait 1998). Altered diversity and composition of earthworms, nematodes, and mites have been used to indicate the changes in soil quality (Bongers 1990; Blair et al. 1996).

The Images model (this volume) predicts the types of land conversion from 1990 to 2050 for each continent (Table 4.4). The North American continent is projected to lose agricultural land, tundra, forests, woodlands, and deserts and gain substantially in regrowth forests, grassland/steppe, grassland, ice, scrub and savanna (Table 4.4). North America's loss of agricultural land is typical of other developed regions (e.g., Europe, Australia, and New Zealand). In contrast, the developing countries are predicted to increase their agricultural land, driving the global increase in agroecosystems. The types of agricultural management practices selected in the future (e.g., slash and burn, rotations, no-tillage with minimal chemical inputs, conventional, intensive monoculture agriculture with high chemical inputs) will determine the extent of impact of this land use change on soil biodiversity (Anderson 1994; Brussaard et al. 1997; Giller et al. 1997; Swift 1997).

Whether agricultural management is based on intensive, high-chemical input or no-till, minimal-chemical input, all types of management result in disturbance to the soil and the biota at local to regional scales. Cultivation, pesticides, increased herbicide use on no-till crops, increases in pests and invasive species, depletion of soil organic matter through erosion, and overuse of land can all affect trophic structure and composition, species abundance, richness, and biomass of soil organisms (Brussaard et al. 1997; Niles and Wall Freckman 1997; Mando 1998). In some groups, however, disturbance results in effects other than a decline in biodiversity. For example, following a disturbance, ant diversity may decline with or without a corresponding increase in individuals, remain unchanged, or increase as opportunists from nearby land invade (Folgarait 1998). The effects of these changes on ecosystem processes and services can be expected to be profound at the regional and continental scales.

Table 4.4. The IMAGES (this volume) projection of land use change from 1990 to 2050. The net land conversion was determined as the area (km²) by which the land type will increase or decrease (–) from 1990 to 2050. The upper figure shows the net land conversion in area (×10³ km²); the lower figure shows the net land conversion as % of 1990 area

	Agricultural land	Extensive grassland	Regrowth forest	Ice	Tundra	Wooded tundra	Boreal forest	Cool conifer forest	Temperate mixed forest	Temperate deciduous forest	Warm mixed forest	Grassland/steppe	Hot desert	Scrubland	Savanna	Tropical woodland	Tropical forest
North America	–554.6	110.7	834.0	70.2	–623.0	–157.8	–52.7	–216.5	–262.7	–316.3	–277.3	1,381.4	–11.2	86.9	8.3	–19.3	0.0
	–14.2	9.4	250.6	36.6	–25.3	–16.2	–1.1	–27.7	–28.9	–59.2	–54.7	84.2	–5.2	104.6	n.a.	–54.0	n.a.
Mexico, Central America, and Caribbean	71.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–58.1	–117.4	146.6	–15.6	–15.1	–12.1
	6.1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	–22.7	–53.8	173.2	–5.6	–7.3	–28.6
South America	564.1	–40.9	364.4	0.0	–47.1	11.2	–48.2	0.0	40.1	4.4	–80.7	–60.1	165.5	–77.0	–621.1	–55.1	–119.3
	11.1	–4.5	n.a.	n.a.	–43.3	46.8	–29.1	n.a.	89.1	37.1	–32.0	–5.7	301.8	–14.6	–25.3	–1.4	–4.3
Europe	–601.5	26.8	430.4	–10.5	–40.4	–54.7	–249.5	24.0	470.7	7.2	1.4	–30.0	2.5	23.6	0.0	0.0	0.0
	–11.8	8.0	89.1	–20.9	–27.1	–42.7	–20.2	3.1	89.7	1.8	1.7	–21.6	n.a.	18.3	n.a.	n.a.	n.a.
Africa	7,127.1	2,472.9	–89.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–56.9	–695.4	–419.7	–1,496.9	–4,364.4	–1,509.3	–967.5
	88.6	88.5	–97.1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	–100.0	–56.4	–4.8	–98.7	–100.0	–100.0	–100.0
Asia	3,975.2	2,011.0	584.2	–62.0	–1,548.3	–269.0	179.3	135.1	–23.7	–235.8	–356.8	–1,351.3	–1,993.7	–244.1	–576.7	–171.1	–52.3
	44.3	36.4	131.0	–62.3	–49.7	–23.9	2.1	31.1	–11.1	–79.5	–92.1	–29.2	–43.4	–50.0	–51.5	–65.2	–53.1
Indonesia and Pacific Islands	565.4	9.1	132.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–24.6	0.0	0.0	0.0	–12.0	–45.7	–624.5
	122.4	12.8	214.9	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	–80.0	n.a.	n.a.	n.a.	–66.8	–51.8	–39.0
Australia and New Zealand	–243.8	318.5	42.2	0.0	–4.4	–2.2	–17.4	0.0	–2.3	–2.5	–36.3	–83.9	–113.0	152.1	–7.1	0.0	0.0
	–8.5	16.9	365.0	n.a.	–100.0	–50.0	–100.0	n.a.	–100.0	–100.0	–100.0	–6.3	–11.3	38.1	–7.4	n.a.	n.a.
Greenland	0.0	0.0	0.0	95.6	–95.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	n.a.	n.a.	n.a.	4.8	–61.2	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Global	10,903.4	4,908.0	2,297.7	93.3	–2,358.9	–472.4	–188.5	–57.4	222.0	–543.0	–831.1	–897.3	–2,487.1	–1,408.9	–5,588.8	–1,815.5	–1,775.6
	30.6	37.9	158.0	4.0	–39.3	–21.0	–1.3	–2.9	13.1	–43.4	–61.3	–8.7	–16.8	–43.6	–67.1	–30.5	–32.3

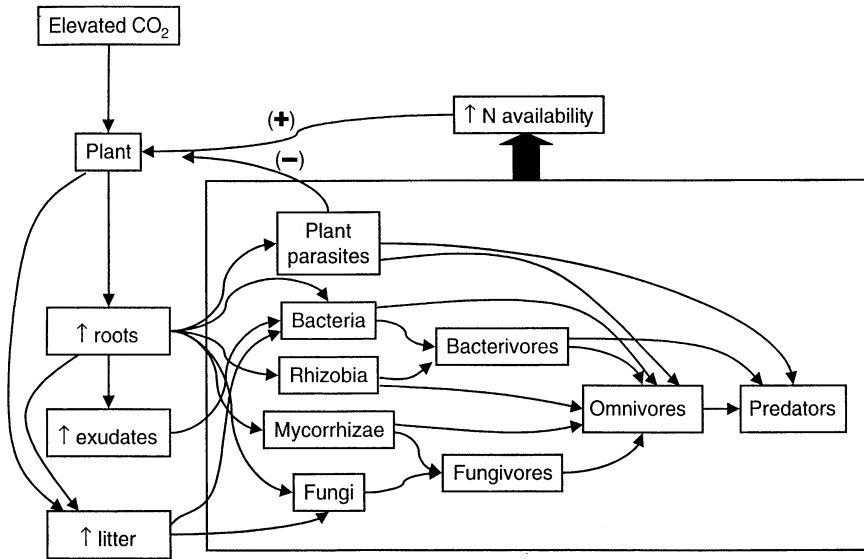


Figure 4.3. Elevated atmospheric CO_2 is likely to influence soil foodwebs indirectly via changes in plant physiology. Figure 4.2 shows the components of soil foodwebs that may be influenced by increases in litter production and root activity. The response of biodiversity of such foodwebs is virtually unstudied. Consequences for biomass may be more reliably predicted (Norby and Cotrufo 1998) and stimulation of microbial-based foodwebs (with positive feedbacks to plant productivity) or of plant parasites (with negative feedbacks to plant productivity) may occur.

Elevated CO_2

Effects of elevated CO_2 on soil biodiversity may be largely indirect via altered vegetation (Yeates et al. 1997; Folgarait 1998; Wolters et al. 2000). Because of the existing high CO_2 concentrations within the soil, direct effects of elevated CO_2 on soil biodiversity have been considered less important than indirect effects (van Veen et al. 1991; O'Neill 1994; Coleman and Crossley 1996; Lavelle et al. 1997; Wolters et al. 2000). This assumption, however, requires further investigation (Sustr and Simek 1996) because gradients as low as 100 ppm CO_2 in the soil atmosphere attract plant parasitic nematodes to roots over distances of several meters (Dusenbery 1987; Pline and Dusenbery 1987). CO_2 also attracts entomopathogenic nematodes to their insect hosts in soil (Barbercheck and Kaya 1991). Indirect effects of elevated CO_2 on soil foodwebs, via an altered supply of plant-based resources, have been studied in more detail than direct effects and could occur with (1) changes in plant species composition, and (2) changes in plant physiology (Fig. 4.3).

The composition of plant communities could be impacted by elevated CO_2 through differential physiological responses of plant species, depending on plant functional group (e.g., C_3/C_4) and capacity for additional carbohydrate

utilization. Plant community composition could change within ecosystems (Korner 1996) or across biomes (Cure and Acock 1986; Oechel et al. 1994; Drake et al. 1996) and could indirectly influence soil biodiversity and ecosystem processes. There are few data, however, on the effects of altered plant species composition due to elevated CO_2 on soil biodiversity.

The effect of elevated CO_2 on plant physiology has been studied in more detail. Elevated CO_2 consistently enhances photosynthesis, at least initially, for a wide variety of plant species (Bazzaz 1990; Korner 1996). The plant physiological changes that may have greatest impact on soil biodiversity are increased net primary productivity (biomass) (Yeates et al. 1997), including an increase in above-ground biomass with increased litter inputs to soil and increased below-ground inputs (noted later); changes in plant tissue quality (Lincoln et al. 1993; Penuelas and Estiarte 1998) increased water use efficiency (Casella et al. 1996; Drake et al. 1997; Jackson et al. 1998) and altered phenology (Bazzaz et al. 1989; Newton et al. 1995). Below-ground plant responses most frequently noted in elevated CO_2 experiments are reallocation of enhanced photosynthate manifested as an enhanced root biomass (especially under water and nutrient limited conditions), increased root length, and rhizodeposition (Stulen and den Hertog 1993; van Noordwijk et al. 1998; Wardle et al. 1998) and root respiration (Boone et al. 1998). There is insufficient evidence to determine whether root turnover increases (Pregitzer et al. 1995; van Noordwijk et al. 1998).

Most data on the response of soil organisms to plant physiological responses has been at the functional group level (O'Neill 1994; Yeates et al. 1997; van Noordwijk et al. 1998; Wardle et al. 1998). These studies indicate that increased below-ground plant resources affect both herbivory and decomposition foodwebs (Zak et al. 1996). Decomposition foodweb responses include an increase (O'Neill et al. 1987; Klironomos et al. 1998) to no change (Yeates and Orchard 1993; Lussenhop et al. 1998) in microbial biomass, increased fungal mass, hyphal length, percent colonization and/or spores, and an increased abundance of fungal feeding microarthropods (Klironomos et al. 1996; Jones et al. 1998; Lussenhop et al. 1998; Rillig et al. 1999), bacterial feeding nematodes (Yeates and Orchard 1993), protozoa (Lussenhop et al. 1998), and enchytraeids (Yeates et al. 1997). The differences in microbial biomass response to elevated CO_2 may in part reflect differences between fungal and bacterial foodwebs. For example, fungal biomass appears to be more consistently enhanced than bacterial biomass, and Diaz (1996) has suggested that this may favor mycorrhizal plant species over nonmycorrhizal species.

Although it has generally been assumed that increases in below-ground resources driving shifts in soil biotic communities under elevated CO_2 are due to reallocation of enhanced photosynthate, other mechanisms should be considered. In non- CO_2 experiments other abiotic and biotic factors have been shown to increase root exudation and cause shifts in microbial composition. Increased leakiness of roots and a substantial increase in the amount of root

exudates can be due to waterlogging and the decreased oxygen availability in soils (Kuan and Erwin 1980), the nematode *Meloidogyne* parasitizing and inciting gall formation in roots (Van Gundy et al. 1977), and “normal” root microflora (Prikryl and Vancura 1980; Jones and Darrah 1993). Elevated CO₂ could potentially alter these factors (e.g., by altering water use efficiency of plants, host susceptibility to parasitism or composition of root microflora, respectively) leading to nonphotosynthate-driven effects on root exudates with consequences for soil biota.

There are few studies of the indirect effect of elevated CO₂ on soil biodiversity at the species level, and the limited data make it difficult to extrapolate findings to regional and global levels. A number of studies have noted shifts in soil species composition under elevated CO₂. Jones et al. (1998) found significant and consistent shifts in soil fungal species composition between Ecotron experiments maintained at ambient and elevated CO₂. Collembola, which are major consumers of fungi and graze selectively on different fungal species, also showed dramatic shifts in species composition.

In a pot experiment Klironomos et al. (1998) found differential responses of mycorrhizal fungi to elevated CO₂, with consequences for the host plant *Artemisia tridentata*. The mycorrhizal species *Glomus intraradices* and *Glomus etunicatu* increased intraradicle structures and spore production, and their host plants showed increased growth under elevated CO₂. Other mycorrhizal fungi, *Acaulospora* sp. and *Scutellospora calospora*, increased extraradicle hyphal length and the host plants showed increased leaf phosphate content, but not growth, under elevated CO₂. The authors suggest that host plants of mycorrhizal species having enhanced phosphate supply under elevated CO₂ may have a longer-term competitive advantage, which is a hypothesis that could be readily tested in field experiments in different biomes.

The increased plant carbon:nitrogen ratio often observed under elevated CO₂ has been hypothesized to reduce plant litter quality and thus alter the soil decomposer community and rates of decomposition. This hypothesis has generally been unsupported (Norby and Cotrufo 1998). There are exceptions, however, such as the reduced quality of ash litter under elevated CO₂ being less palatable to the woodlouse *Oniscus asellus* (Cotrufo et al. 1998). Changes under elevated CO₂ in the amount of litter or in plant phenology (e.g., relative proportions and timing of leaf, stem, root, fruit, and woody litter) may be more likely than altered litter quality and could have profound effects on soil species and decomposition rates (Andrén et al. 1995; Norby and Cotrufo 1998).

CO₂-induced changes in above-ground, living plant tissue chemistry has significant effects on above-ground herbivores (see Lincoln et al. 1993; Penuelas and Estiarte 1998); below ground, however, there is little evidence of CO₂-induced changes in root quality (Van Ginkel et al. 1996; Jones et al. 1998) affecting herbivores (van Noordwijk et al. 1998). Differences in root quality in nonelevated CO₂ experiments, however, have had significant effects

on plant pathogenic soil species, and there is strong circumstantial evidence for co-evolution of root chemistry and root herbivores, which suggests that CO₂-induced changes in root chemistry might have significant impacts on herbivorous soil biota (Wallace 1963; van Noordwijk et al. 1998; Wardle et al. 1998).

Biotic Introductions

Introductions of above-ground or below-ground plant or animal species can change soil structure, soil chemistry, soil biotic communities (Mamiya 1983; Rutherford et al. 1990; Boag et al. 1997; Burtelow et al. 1998; Folgarait 1998; Fraser and Boag 1998; Ehrenfeld 1999), and nutrient cycling (Vitousek et al. 1987). Dispersal of soil-invasive species into new habitats occurs with transport of soil attached to plants, vertebrates (e.g., cattle, birds, zoo animals) and invertebrates, field and construction machinery, and wind erosion of soils. In addition, movement of soil through irrigation and flooding is a source of soil organism dispersal on a local to regional scale.

The introduction of exotic plant species can have unexpected effects on soils and soil biodiversity. Invasion of nitrogen-fixing symbiotic bacteria with the tree, *Myrica faya*, changed the nutrient cycling and organic matter status of the Hawaiian ecosystem (Vitousek et al. 1987). The introduction of two exotic plant species, *Berberis thunbergii* and *Microstegium vimineum* in the northeastern United States, resulted in soils with higher pH, a thinner litter layer and organic horizon, and higher populations of earthworms (Kourtev et al. 1998). Kourtev et al. (1998) speculated that the exotic plants created a more favorable soil environment for earthworms than uninvaded soils. The resulting larger populations of earthworms may have incorporated more litter that resulted in the decrease in organic matter.

Introductions of exotic soil macroinvertebrates can cause major changes to soil habitat characteristics (Folgarait 1998) and will change the species composition of mesofauna (e.g., mites, Collembola, nematodes, and protozoa). Ant and earthworm species, with different biologies than the indigenous community, can alter distribution of organic matter, soil aeration, water infiltration, and soil chemistry (Lee 1985; Lavelle et al. 1997; Burtelow et al. 1998; Folgarait 1998), affecting soil biodiversity and ecosystem processes. Lee (1961) recognized that the major threats to earthworms were habitat degradation and invasion of exotic competitors. Lee has more recently implored scientists and others to preserve whole ecosystems and to gather scientific experimental data on impacts of invasive species on soils and ecosystem processes (Lee 1999; see also James 1995). Invasions of Australasian planarian flatworms, which have no known beneficial effects on soils but are obligate predators of earthworms, are causing great concern in the United Kingdom and northern Europe (Boag et al. 1997; Fraser and Boag 1998). All flatworm species in North America are introduced (Ogren and Kawakatsu 1998), but there is little information on their ecology and effect on ecosystem processes.

The invasive species in soils have had major effects on economies of nations. Some microscopic species of soil bacteria, fungi and plant parasitic nematodes have been subject to state, national and international quarantine regulations for decades. For example, the nematode species *Bursaphelenchus xylophilus* (Table 4.3) introduced from North America to Japan and then Portugal (Mota 1999), is capable of killing pine tree plantations and forests in less than 6 weeks and is subject to quarantine regulations (Mamiya 1983; Rutherford et al. 1990). These illustrations show that the introductions of plants and soil biota can have important, costly impacts on soil biodiversity, soil structure and fertility, and ecosystem processes at regional and global scales. Initiatives for global programs on species invasions must consider the impacts on soil systems as a priority.

Nitrogen Deposition

Nitrogen deposition can have major effects on the biodiversity of soil communities because of its indirect effects on vegetation (e.g., changes in plant productivity, plant quality, and plant composition) and direct effects through acidification of the soil habitat. Major taxonomic groups have differential responses to acid deposition, and some evidence also exists for shifts in diversity at the functional group and species level. We expect enchytraeids, earthworms, mesofaunal groups, and microbial groups to be most influenced because of the acidification of the soil. Nematode and microarthropod functional groups are viewed as good indicators of the effects of acid deposition on soils (Van Straalen et al. 1988).

At a regional and global scale, the effect of nitrogen deposition may be strongly modified by the production potential of the ecosystem (Vitousek et al. 1997). When ecosystems have a high productivity potential, nitrogen deposition may increase the productivity of existing plant species rather than directly altering plant species composition (Vitousek et al. 1997); thus, effects on soil biota will be through altered amounts and quality of resource inputs from already existing plant species. In ecosystems adapted to low nitrogen availability, increased N deposition may dramatically alter plant species composition (Wedin and Tilman 1996; Vitousek et al. 1997) with consequences for soil biotic composition (Berg and Verhoef 1998).

Studies of acidification effects on soil biota have often considered acidification effects due to sulphate, as well as nitrogen deposition. Many studies are from forest ecosystems where declines in abundance and shifts in community composition of earthworms, enchytraeids, nematodes, bacteria, and fungi have been observed (Huhta 1984; Bewley and Parkinson 1986; Van Straalen et al. 1988; Persson et al. 1989; Baath et al. 1990; Hyvonen and Persson 1990; Ruess 1995). Long-term studies in the Tatra Mountains of Slovakia showed that vegetation and soil biodiversity changed with acid deposition (Rusek 1993). Collembolan species that were rare in 1977 became

abundant and widespread in distribution by 1990. In contrast, some previously abundant collembolan species have totally disappeared from the region. Vegetation patterns shifted as a result of acid deposition, and collembolan species composition became more homogenous and less diverse at the landscape scale.

Insights on the effect of nitrogen deposition on soil species diversity may also be gained from studies of additions of inorganic fertilizer to soils, although fertilization, in contrast to atmospheric nitrogen deposition, involves sudden and often larger nitrogen inputs. At the functional level, nitrogen fertilization appears to stimulate root herbivory- and bacterial-based foodwebs (Gupta 1994). At the species level, inorganic N fertilization increased (Lehle and Funke 1989) or had no effect on protozoan diversity (Berger et al. 1986). It also decreased the diversity of microarthropods (Siepel and Van de Bund 1988).

Soil Warming

Predictions of future temperature and precipitation are less certain than predictions of atmospheric CO₂ concentrations and land use change. In general, predictions suggest an increase in mean global temperature of 1–3.5°C, increased precipitation (with regional variation), and increased severity and frequency of catastrophic climatic events (Acosta et al. 1998). The predicted climate changes may affect soil biotic diversity directly by altering soil temperature, moisture, and wet-drying and freeze-thawing cycles, or indirectly by altering vegetation community and productivity, and the amount and timing of decomposition (Hodkinson et al. 1998; Sohlenius and Bostrom 1999). Young et al. (1998) predict that these changes in vegetation may alter soil biodiversity through changes in soil carbon content and spatial heterogeneity of soil structure.

These climatic effects would be predicted to affect most strongly organisms that presently live at extremes of climate tolerance ranges. For example, enchytraeid species, which are cold tolerant and key taxa in acid soils of polar regions, might decline at high latitudes with increased frequency of climatic events that affect soil temperature, moisture, and freeze-thaw cycles (Somme and Birkemoe 1997; Huhta et al. 1998).

The soil biotic response to warming may strongly interact with moisture availability, at both regional and local scales. At regional scales, under warmer drier conditions, grasslands may increase, and their rhizome-associated, aggregating microorganisms may increase soil aggregates and biodiversity. In contrast, warmer wetter conditions may increase rainforests, and the soil aggregating, biodiversity-promoting microorganisms of grasslands may be lost (Young et al. 1998). At a local scale, shifts in species composition of soil biota in response to warming may also be strongly influenced by moisture. Enchytraeid species that were able to migrate through the soil profile to moist

areas (*Cognettia sphagnetorum*) or which could tolerate dry conditions (*Achaeta eiseni*) generally increased at a +2.5°C warmer site, whereas one other species (*Cernosvitoviella atrata*) was unable to avoid dry conditions and suffered severe mortality at the increased temperature (Briones et al. 1997). The more tolerant and mobile species could also withstand the “extreme” summer temperatures at the warmer site. Biodiversity at higher taxonomic levels than species was also influenced by temperature and moisture interactions. Briones et al. (1997) demonstrated that Dipteran larvae died under warmer and drier conditions, but tardigrades survived, probably in an anhydrobiotic survival state. Studies of Collembola and oribatid mites also demonstrated that, when moisture is limiting, differential responses to temperature at species and higher taxonomic levels can become apparent. In dry conditions in both the laboratory (Hodkinson et al. 1996) and arctic field sites (dry semi-polar desert as opposed to moist tundra) (Coulson et al. 1996) increased temperature resulted in a decline in Collembola, but not in oribatid mite densities. Differential species responses also occurred within these groups.

Effects of warming may be large in those ecosystems that are currently limited by temperature such as the arctic tundra and semi-polar deserts (Swift et al. 1998). For most soil micro- and mesofaunal groups, arctic regions currently contain less than 15% of the species biodiversity of temperate ecosystems. It might therefore be predicted that an increase in temperature would alleviate much of this limitation (Swift et al. 1998); however, the studies of Collembola and oribatid mites described earlier (Coulson et al. 1993; Coulson et al. 1996; Hodkinson et al. 1996; Hodkinson et al. 1998) reveal that, as long as there is sufficient moisture, cryotolerant organisms in arctic regions may be well adapted to fluctuating temperatures, and population densities will be little affected by soil warming. Even small microscopic invertebrates have mechanisms for survival of temperature extremes (Crawford 1981; Coleman and Crossley 1996).

Few studies have investigated the effects of soil warming on biota in temperate regions, especially at the species level. One warming study in a Northern Michigan sugar maple forest noted shifts in microbial function and composition at higher taxonomic levels that may have important consequences for the organic matter substrate pool and ecosystem functioning (Zogg et al. 1997). The potential effects of such dramatic responses on soil species will require further investigation.

The preceding studies reveal considerable differences in the response of soil organisms to soil warming, but we presently have too little data to determine how these will impact soil biodiversity and ecosystem functioning at large spatial scales. It is also clear that many interacting factors (e.g., the microclimate produced by vegetation, and the structure of the soil that determines its capacity to provide refuges from drought and/or to maintain moisture) will strongly influence an organism's response to soil warming. These interacting factors will in turn be strongly influenced by the other drivers of global change; we must strive to consider their effects simultaneously.

Conclusions

Land use change is expected to be the primary global change driver affecting soil biodiversity. Elevated CO₂ and biotic introductions will have major impacts on soil species and ecosystem services. All drivers, including nitrogen deposition and warming, are likely to show strong interactions with each other. Few studies have directly investigated the effects of global change drivers on soil biota, compared with the evidence accumulating for above-ground biota. Nevertheless, there is sufficient evidence from microcosm and field experiments investigating either effects of single global change drivers, or effects of disturbances on soils similar to those predicted under global change to predict that global change drivers will disrupt current species assemblages within and across functional groups.

To ascertain whether these changes in soil biodiversity will have long-lasting effects on ecosystem functioning will require testing of hypotheses on the relationship between soil species and ecosystem function, collaboration of scientists in many disciplines, and incorporation of technologies at microsite to regional scales. GIS maps of soil textures, soil carbon, vegetation, and moisture can be used to predict areas where there is high soil biodiversity and productivity, where soils and biota are vulnerable to change, and where plant pathogens may spread. We believe syntheses of available results, and future experiments across soil disciplines of agriculture and ecosystem science, should be designed to provide us, as quickly as possible, the information necessary for judicious decisions on the future sustainability of the world's soils and the world's life in soils.

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